

PRELIMINARY REPORT OF UPPER CRETACEOUS ANGIOSPERM REPRODUCTIVE ORGANS FROM SWEDEN AND THEIR LEVEL OF ORGANIZATION¹

E. M. FRIIS²

ABSTRACT

Well-preserved fossil angiosperm reproductive organs from the Upper Cretaceous of Sweden provide increased knowledge of structure and evolutionary relationships of Cretaceous angiosperms. The material includes a diverse assemblage of angiosperm flowers, fruits, seeds, and anthers representing more than 100 taxa. This paper focuses on the level of organization of the reproductive organs with special attention directed to the various types of flowers. The flowers are all very small, usually actinomorphic and bisexual. The position of the perianth is hypogynous or, more commonly, epigynous. Some of the flowers are of simple construction with only one whorl of perianth parts, apparently adapted to wind-pollination. Others have well-developed calyx and corolla, sometimes together with the presence of a disk, suggesting adaption to insect-pollination. A number of floral diagrams are presented for the fossil flowers of Sweden, and their systematical position is discussed.

Theories of evolutionary relationships within the angiosperms are largely based on comparative studies of the flower structure. The study of fossil flowers is therefore essential to the understanding of the origin and evolution of the angiosperms. However, angiosperm flowers are rare in the fossil record, and less than 200 species have been described so far.

The amount of information obtainable from these fossils is variable, depending largely on the mode of preservation. Floral structures and arrangement of parts are best studied in three-dimensionally preserved flowers, but few flowers are known in this state of preservation. Plant material usually has collapsed in varying degree during incorporation into sediments and so becomes preserved as compressions or, if completely decayed, as impressions. Such material usually yields very incomplete information on the floral details, but the recent application of transfer techniques and electron microscopy has revealed the considerable potential for studies of compressed flowers such as those from the Eocene of North America (Crepet & Dilcher, 1977; Crepet & Daghljan, 1980; Crepet et al., 1980; Daghljan et al., 1980).

The majority of fossil flowers are known from Tertiary deposits, and only about 20 different species have been described from the Cretaceous. The most important source of information on Tertiary fossil flowers is probably the Paleogene Baltic Amber, which accounts for about one-third of the known record. Owing to the amorphous texture of the amber and that it was fluid at the time of incorporation of the fossils, very fine details have been preserved (Goeppert & Berendt, 1845; Caspary, 1872, 1881a, 1881b; Conwentz, 1886; Larsson, 1978). The amber fossils are strictly molds, with very little organic material remaining, and thus anatomical details are scarce. Because of extensive information existing on the morphology and the structure of the fossils, however, it has been possible to establish the botanical affinity for a large proportion of the amber flowers (Conwentz, 1886).

Anatomical information is usually obtainable from petrifications, but reconstructions of arrangement of parts may be surprisingly problematic, and establishment of the botanical affinity is often uncertain. One of the few petrified flowers is *Palaeorosa similkameensis* Basinger (1976) from the Eocene of British Columbia. This is

¹ I am grateful to W. G. Chaloner, P. Crane, R. Dahlgren, D. L. Dilcher, H. Friis, and K. Raunsgaard Pedersen for encouragement during the study and for constructive criticisms of the typescript, and to A. Skarby for providing samples from Åsen. L. Eklund-Jürgensen and J. Sommer are thanked for their help in preparing the typescript and plates. H. J. Hansen is thanked for the permission to use the scanning electron microscope at the Geological Department, University of Copenhagen. I gratefully acknowledge the receipt of a research fellowship from the British Council and from the Danish Natural Science Research Council.

² Geologisk Institut, Aarhus Universitet, Universitetsparken 8000, Aarhus C, Denmark.

probably the most fully known of these petrified structures. Few other species were described from the Intertrappean beds in Deccan, India, probably of Eocene age (Shukla, 1944; Prakash, 1956; Chitale & Patel, 1975, for example). *Cretovarium japonicum* Stopes & Fujii (1911) is imperfectly preserved but is significant in being the only petrified floral structure described from the Cretaceous.

No fossil angiospermous flowers have been described yet from the Lower Cretaceous, but from fossil fructifications we know that reproductive structures were diverse by the late early Cretaceous (Dilcher et al., 1976; Dilcher, 1979; Vachrameev & Krassilov, 1979). In the early Upper Cretaceous (Cenomanian) the diversity is documented by fruiting as well as floral structures from Europe (Velenovský, 1889; Bayer, 1914; Velenovský & Viniklár, 1926, 1927, 1929, 1931) and from North America (Dilcher, 1979; Dilcher & Basinger, 1980; Dilcher & Crane, 1984; Crane & Dilcher, 1984).

From the Uppermost Cretaceous (Senonian), small angiosperm flowers have recently been discovered from eastern North America (Tiffney, 1982 and pers. comm.; Hueber, pers. comm.) and from Scania, southern Sweden (Friis & Skarby, 1981, 1982; Friis, 1983). This review is an attempt to illustrate the diversity in structure of the Upper Cretaceous angiosperms based on the study of the well-preserved Swedish material. Special attention is directed to the various organizational levels of the fossil flowers, and floral diagrams of the main basic types are presented (Figs. 1–9). Although the taxonomic study of the Swedish material is still at an early stage, it has been possible to demonstrate relationships between some of the fossil taxa and modern plant groups at the family or ordinal level.

MATERIAL

The angiosperm fossils described here were collected from the upper part of the fluvial sequence in Höganäs AB's clay pit at Åsen, southern Sweden. The age of the sediments is probably Upper Santonian or Lower Campanian (Friis & Skarby, 1982).

The fossils were obtained from unconsolidated clays and sands by sieving in water. They were then cleaned in hydrofluoric and hydrochloric acid.

The material comprises a diverse assemblage

of leaf fragments, twigs, megaspores, sporangia, flowers, fruits, seeds, and anthers (Friis & Skarby, 1981, 1982; Friis, 1983). The majority of fossils represents angiospermous plants, and more than 100 taxa have so far been recognized. The commonest of the angiosperm fossils are fruits and seeds, but the floral structures also constitute an important element of the flora.

The fossils are mainly preserved as three-dimensional charcoal fossils, probably formed as a result of a forest fire (Friis & Skarby, 1981). Their excellent preservation allows detailed study of arrangement of parts. However, the material shows certain limitations. The fossil flowers are generally found isolated from the rest of the plant and the orientation and inflorescence structure is thus unknown. The lack of parts in some flowers may be primary, but could also be caused by shedding before fossilization. Very delicate or protruding parts such as stamens and petals may be broken in open flowers and the study of such parts is often referred to fragments or scars or to flower buds when present. In spite of these limitations, the material yields useful information on the organization of the flower structure reached by the uppermost Cretaceous and represents a significant addition to the known record of angiosperm flowers.

DIMENSIONS OF THE ANGIOSPERM FOSSILS FROM SWEDEN

The fossil angiosperm flowers, fruits, and seeds from Åsen are all of small size, the largest flower being about 4 mm long, and the dimensions of the fruits and seeds range from 0.2 to 5 mm. No fragments of larger fruits and seeds have been observed among the fossils, but larger fragments of twigs and wood are common in some samples. The size distribution of the fossils is apparently independent of the texture of the sediment and the absence of larger fruits and seeds cannot be explained by sorting.

The small size of the Swedish fossils is consistent with the dimensions quoted for fruits and seeds of most other Upper Cretaceous floras of Europe (Vangerow, 1954; Knobloch, 1964, 1971, 1977; Colin, 1973; Jung et al., 1978), Greenland (Miner, 1935), and North America (Schemel, 1950; Hall, 1963). A few fossil floras including large angiosperm fruits and seeds have been reported from the Cenomanian of Europe (Velenovský & Viniklár, 1926) and North America

(Dilcher, 1979), and from the Upper Campanian or Maastrichtian of Africa (Monteillet & Lappartient, 1981).

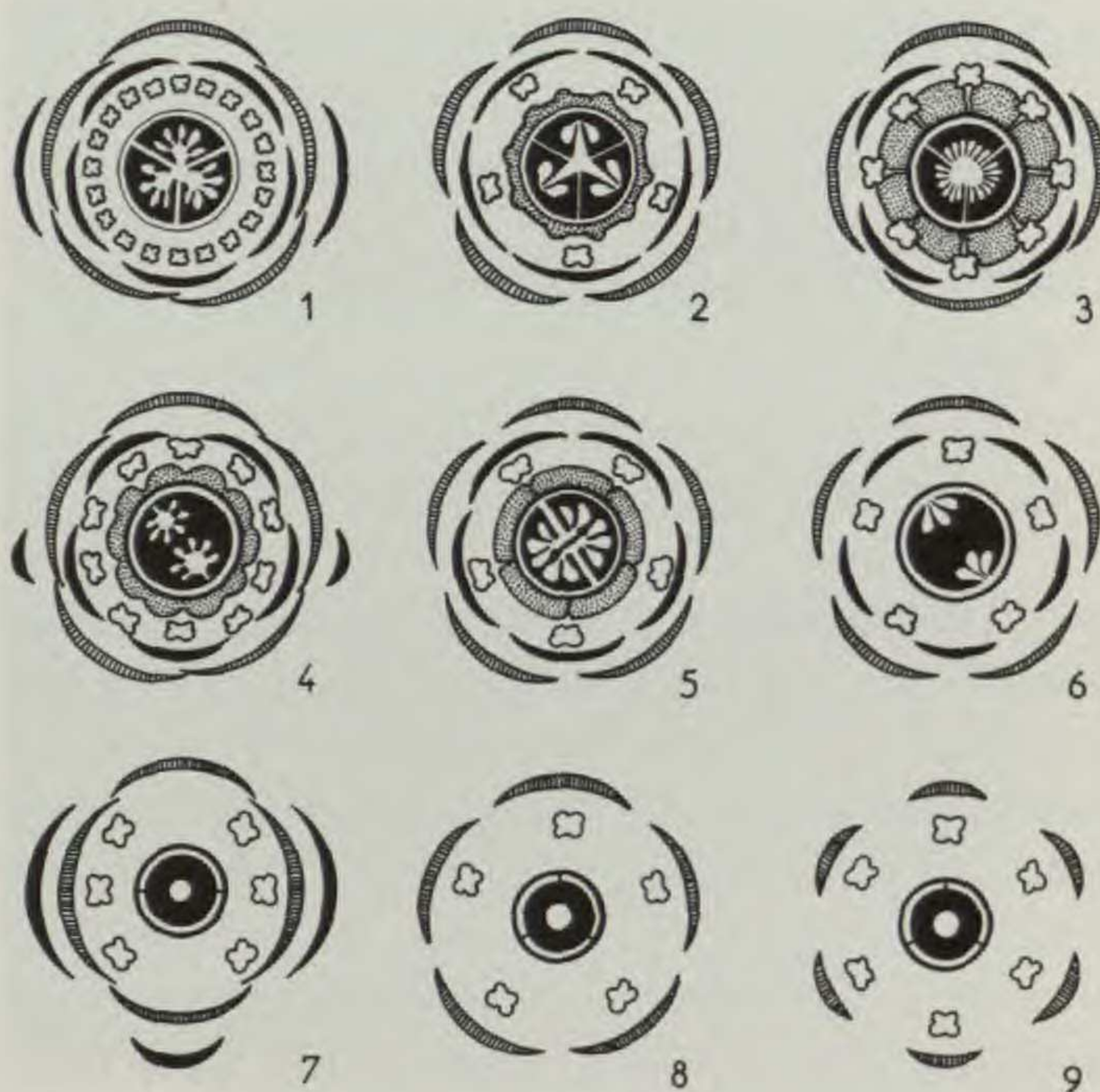
In Recent plants very small seeds are characteristic of epiphytes, saprophytes, and parasites. Small seeds are also common among herbs as well as woody plants inhabiting open country and are especially common in plants of early stages in vegetation succession (Harper et al., 1970; Stebbins, 1974). It is possible that the small size of the fossil fruits and seeds in many of the Cretaceous floras might be explained by paleoecological conditions. However, a number of other factors should also be considered (see Tiffney, 1984).

LEVEL OF ORGANIZATION OF THE FOSSIL FLOWERS FROM SWEDEN

The Swedish material includes more than 20 different floral structures. The fossil flowers are apparently all bisexual and cyclic with a definite number of parts in each whorl. The perianth is well developed in the majority of the flowers, differentiated into calyx and corolla (heterochlamydous), or consisting of only one perianth whorl (monochlamydous). A single fossil flower type is apparently naked (achlamydous or apochlamydous). The position of the perianth is hypogynous or more commonly epigynous. A variety of fruit types has been recognized, including follicles, capsules, nuts, and drupes. There is a great diversity in number of locules, placentation, and number of seeds. The vast majority of the seeds are anatropous. So far only a few orthotropous and amphitropous taxa have been found. The seed coat varies from a thin membranous layer, apparently formed from one integument, to a thick, sclerenchymatous wall formed from one or two integuments.

Some of the basic floral types found in the Swedish material are described below more closely, including, if possible, description of fruits and seeds; the organizational level of the different flowers is illustrated with floral diagrams, and their systematical position is discussed.

1. *Heterochlamydous flowers.* Flowers with well-developed calyx and corolla are the most common among the Swedish floral structures. They are all actinomorphic, including hypogynous as well as epigynous flowers. The sepals and petals are generally free, but in a few flowers the sepals are fused at the bases. Some of the flowers



FIGURES 1-9. Floral diagrams of the basic floral types found among the Upper Cretaceous fossils from Åsen, Sweden.—1-2. Heterochlamydous, hypogynous flowers.—3-6. Heterochlamydous, epigynous flowers.—7-9. Monochlamydous, epigynous flowers.

bear a disk and were probably nectar producing, adapted to insect-pollination. The flowers are generally pentamerous (Figs. 1, 2, 4-6). One flower type differs in being tetramerous (Fig. 3), and a small triangular fruit with persistent calyx indicates that also trimerous floral types were present.

1.1. *Hypogynous flowers with multistaminal androecium.* One fossil genus including hypogynous flowers with a multistaminal androecium has been recovered among the Swedish fossils (Figs. 1, 10-13). It is represented mostly by fragmentary specimens. The flowers are small, about 4 mm long, borne on a thick peduncle. There are two thick bracteoles, five free, coriaceous sepals (Figs. 12, 13), and five free petals. The androecium is composed of 20 stamens in one whorl. The filaments are broad with slightly narrowing bases and a pronounced contraction at the apex. The anthers are elongated and almost as long as the filaments; they are apparently ventrifixed and open by longitudinal slits (Fig. 11). The surface of the anthers has distinctive epidermal cells and short, spiny hairs (Fig. 11). None of the anthers have pollen preserved. The ovary is superior and three-loculed (Fig. 13), formed by three carpels and with three free styles. The surface of the ovary is covered with densely spaced, stiff hairs.

Each locule contains many ovules on pronounced, axile placentae. The characters of the fossil flowers seem to indicate a relationship with modern plants of the Theales, such as members of the Ternstroemiaceae (Theaceae).

Three-loculed capsules with a hairy surface, similar to that of the ovary in the fossil flowers, may represent the mature fruits of similar flowers. They enclose many small seeds. The same seed type is very common in the samples from Åsen, found separate from the fruits. The seeds are about 1 mm long, anatropous, with a distinct raphe, micropyle, and chalaza (Figs. 18–20). The seed coat is composed of two layers of cells. The outer epidermis is built of thick-walled cells with strongly pitted cell walls. Several different species, probably referable to a single genus, have been recognized. The species may be distinguished from each other by the size and shape of the surface cells, the number of cell rows, and the thickness of the seed coat. Two different species are shown in Figures 18 and 20. The organization and structure of the fossil fruits and seeds also seem to indicate a relationship with some modern Theaceae. Although campylotropous or amphitropous seeds are the most common seed type among modern Theaceae, anatropous seeds are found in some genera. The outer epidermis of

the seed coat in many modern Theaceae is similar to that seen in the fossil seeds in having thickened and strongly pitted cell walls.

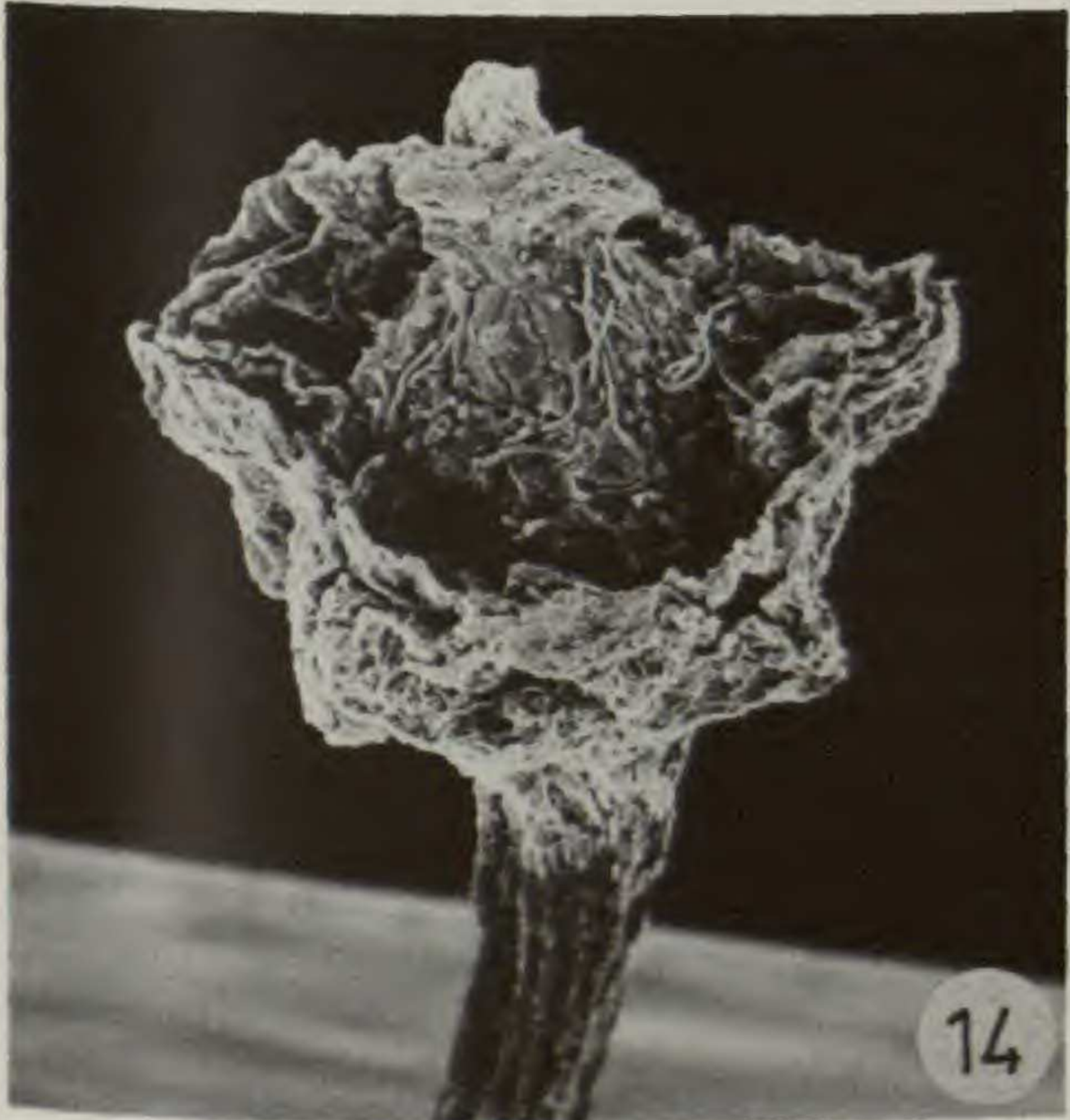
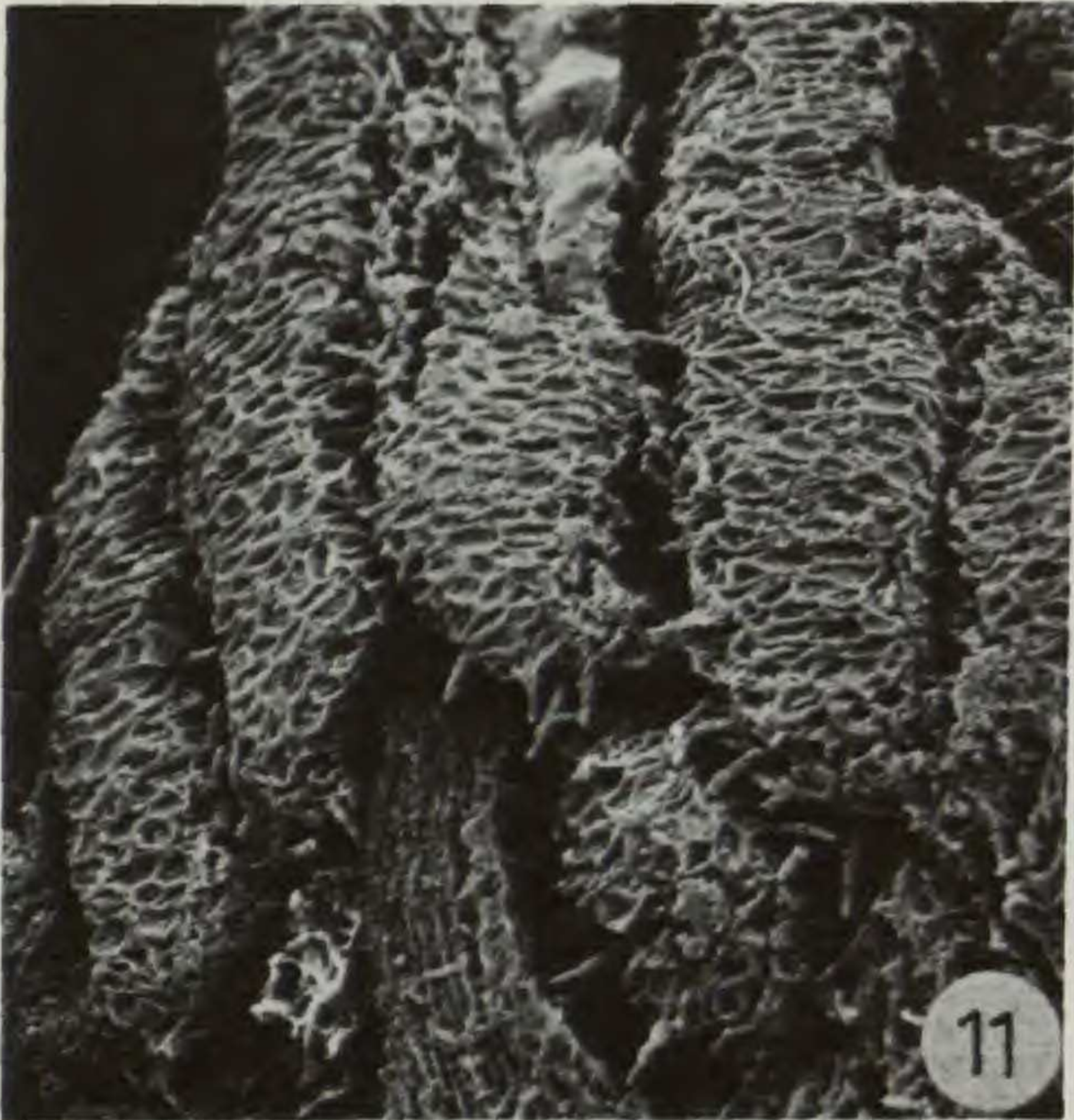
Another group of seeds possibly related to the Theaceae has been recovered among the Swedish fossils. The seeds are anatropous and about 1.5 mm long. The raphe is embedded in the sclerotic mesotesta (Fig. 22). The embryo cavity is elongated ellipsoidal in shape, marked on the outer surface by distinct cell rows (Fig. 21). The inner layer of testa consists of lignified cells with angular lumina, which suggests that they once contained inorganic crystals. Similar seed types also occur in the Lythraceae, but the fossil seems to differ from members of this family by the lack of a fibrous inner layer.

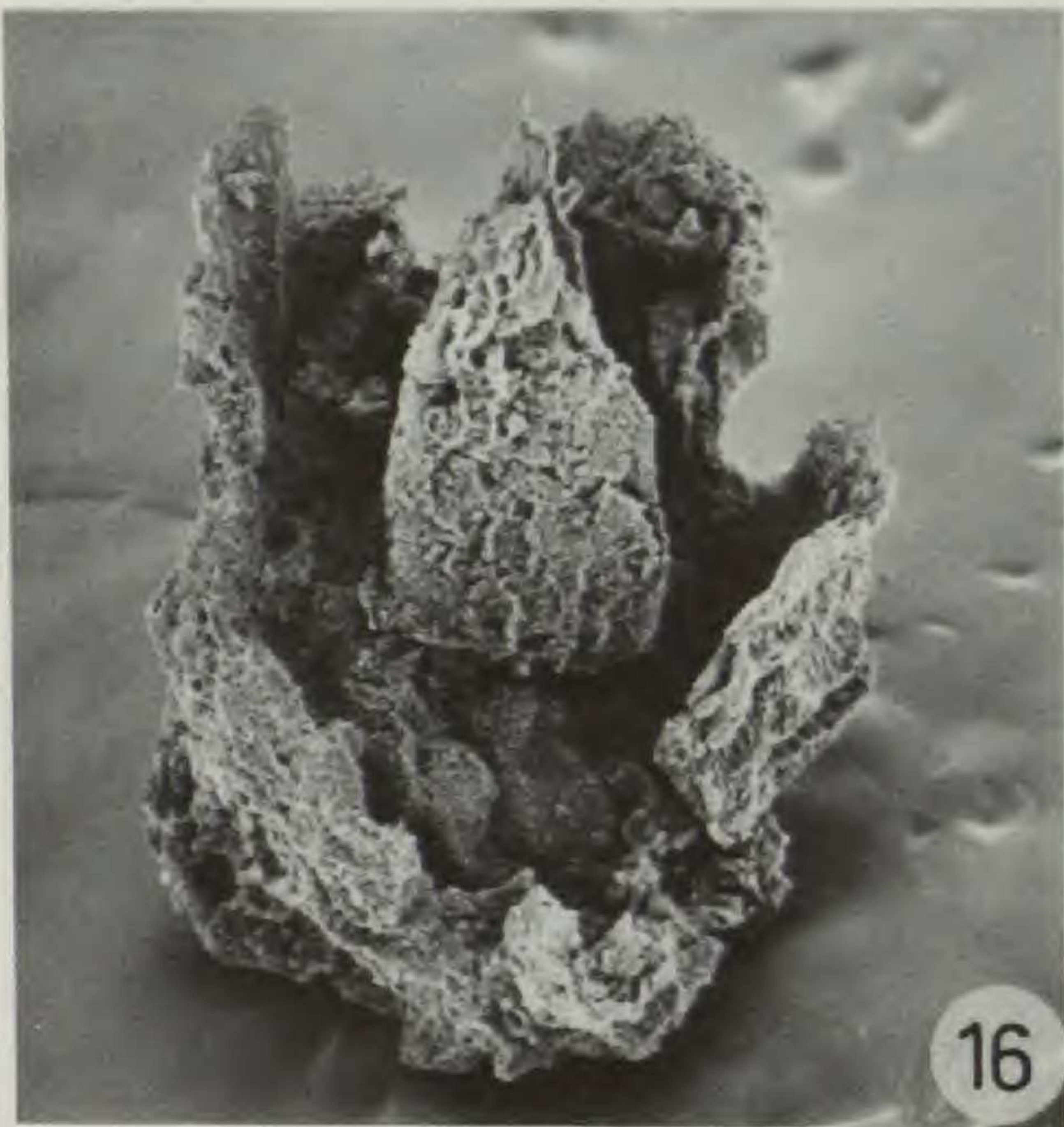
1.2. *Hypogynous flowers with haplostemonous androecium.* A few other hypogynous, pentamerous floral structures are present in the fossil flora, but they are mostly incompletely preserved, and reconstructions of the complete structures have not yet been possible. One of these flowers is shown in Figures 16 and 17. It has five elongated, coriaceous sepals, fused in the basal part, and apparently five petals and five stamens. The ovary is composed of three fused carpels and there are three pronounced, plate-like placentae with many anatropous ovules. At

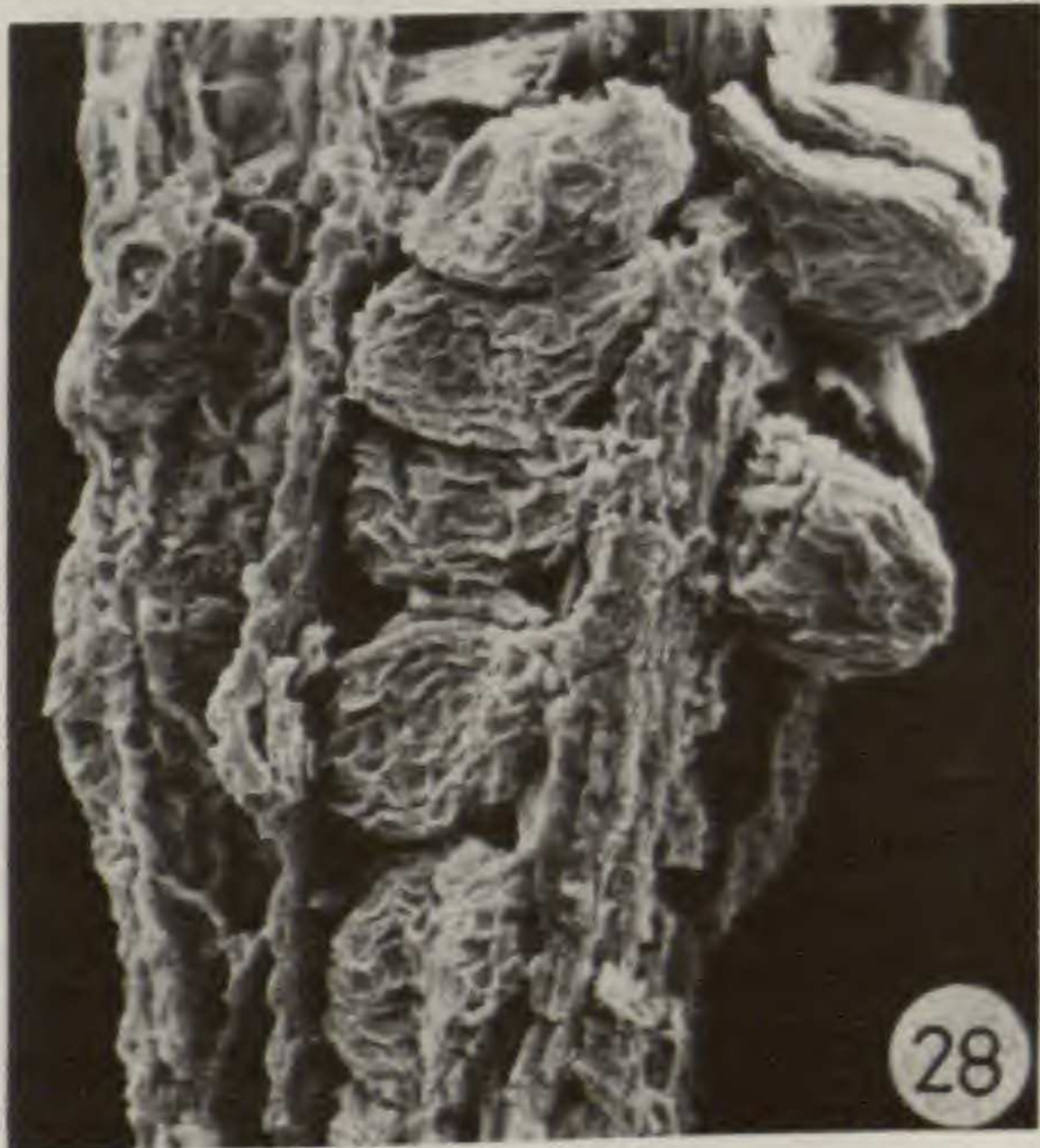
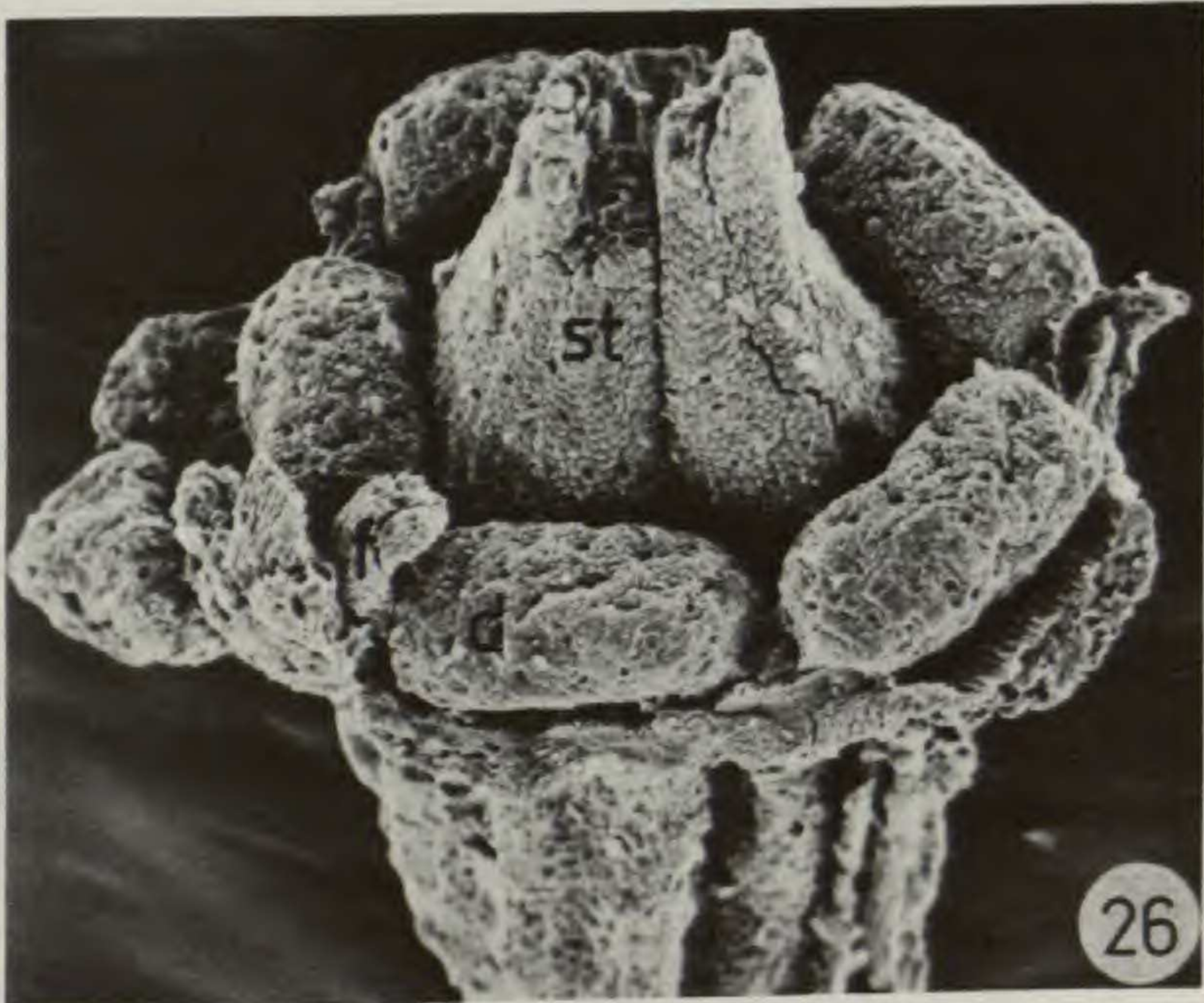
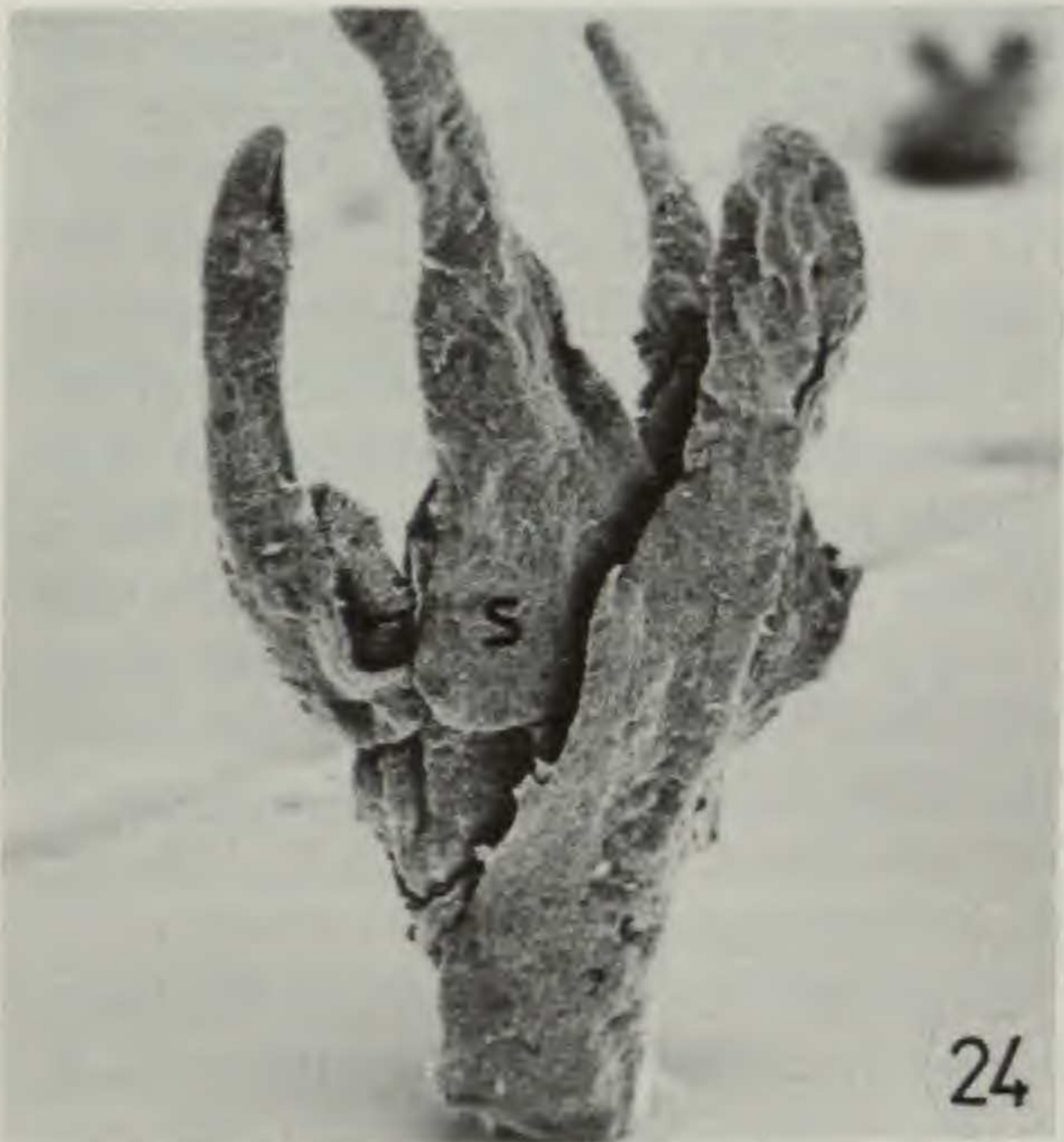
FIGURES 10–15. Fossil flowers from the Upper Cretaceous of Sweden. 10–13. Heterochlamydous, hypogynous flower with multistaminal androecium (floral diagram see Fig. 1).—10. Flower with stamens preserved (a = anther, f = filament); SEM-136₁, ×40.—11. Stamens enlarged showing hairy surface of anthers, ×175.—12. Flower with ovary partly preserved showing coriaceous sepals and bracts; SEM-202, ×25.—13. Ovary enlarged showing three locules and many ovules; same specimen as Figure 12, ×45.—14. Small perigynous flower with hairy ovary and three stigmas preserved; SEM-209₃, ×70.—15. Pollen from surface of ovary; same specimen as Figure 14, ×3,500.

FIGURES 16–22. Fossil flowers and seeds from the Upper Cretaceous of Sweden. 16–17. Heterochlamydous and hypogynous flower with haplostemonous androecium (floral diagram see Fig. 2).—16. Specimen with ovary and sepals partly preserved; SEM-196₁, ×60.—17. Specimen with floral parts abraded showing ten-lobed disk surrounding tripartite gynoecium; SEM-197₃, ×65.—18–20. Anatropous seeds probably related to the Theaceae.—18. External view of seed with narrow surface cells; SEM-130₂, ×65.—19. Internal view of seed similar to Figure 18, showing hilum (h), raphe (r), chalaza (ch), and micropyle (m); SEM-130₆, ×65.—20. External view of seed with large surface cells; SEM-163₁, ×65. 21–22. Anatropous seeds probably related to the Theaceae.—21. External view of seed showing surface cells; SEM-206₄, ×40.—22. Section of seed showing raphe (r) and embryo cavity (e); SEM-206₂, ×35.

FIGURES 23–28. Fossil flowers from the Upper Cretaceous of Sweden related to the Saxifragales. (a = anthers; d = disk; f = filament; p = petal; s = sepal; st = style). 23–24. *Scandianthus* Friis & Skarby, heterochlamydous and epigynous flowers (floral diagram see Fig. 4).—23. *Scandianthus costatus* Friis & Skarby; SEM-210₂, ×55.—24. *Scandianthus major* Friis & Skarby; SEM-210₁, ×30. 25–28. Heterochlamydous, epigynous flower with haplostemonous androecium (floral diagram see Fig. 5).—25. Imperfectly preserved flower bud showing stamens and styles; SEM-181₁, ×50.—26. Flower showing disk, sepals, remnants of stamens and styles; SEM-189₅, ×80.—27. Stamen enlarged; same specimen as Figure 25; ×190.—28. Section of ovary showing many anatropous ovules on axile placenta; SEM-189₂, ×155.







the base of the ovary there is a ten-lobed disk (Fig. 17). A preliminary floral diagram of the fossil flower is shown in Figure 2.

Two or three other pentamerous flowers with their ovary composed of three carpels have been found. A single hypogynous type with a pentamerous gynoecium has also been recognized. Figure 14 shows a minute perigynous flower, about 1.2 mm long with three stigmatic branches and a hairy ovary. Several tricolporate pollen grains have been observed on the surface of the ovary. This type is represented by a few, incompletely preserved specimens and their botanical affinity has not yet been examined.

1.3. Epigynous flowers with diplostemonous androecium. 1.3.1. Pentamerous flowers. Probably the most fully known flowers from the Cretaceous of Sweden are those of *Scandianthus* Friis & Skarby (1982). The flowers are small, about 1–2.5 mm long, bisexual, with radial symmetry (Figs. 4, 23, 24). They are epigynous with five free sepals and five free petals (Figs. 23, 24). There are ten stamens in two whorls, diplostemonously arranged. The anthers are dorsifixed and open by longitudinal slits. The pollen grains are small, about 10 microns in diameter, tricolporate, and tectate. There is a pronounced ten-lobed disk between the stamens and the gynoecium. The ovary is inferior and unilocular, formed by two fused carpels, and with two free styles. The placentae are apical-parietal and pendant, with many anatropous ovules. The fruit is a capsule dehiscing apically between the styles. The seeds are small, about 0.2 mm long, with a thin seed coat possibly formed by only one integument. The presence of a disk and the very small size of the pollen grains suggest that the fossil flowers were insect-pollinated.

Small insect-pollinated flowers of similar construction are common in a number of modern Saxifragalean families, and comparison with modern plant groups indicates a close relationship to the Saxifragales. The best correlation is with members of the families Hydrangeaceae, Vahliaceae, Escalloniaceae, and Saxifragaceae (Friis & Skarby, 1981, 1982). Although the most common organization of the androecium within the Saxifragales is obdiplostemonous or haplostemonous, diplostemonous types occur within the group.

1.3.2. Tetramerous flowers. A single tetramerous flower type has been recovered among the Swedish fossils (Figs. 3, 35, 36). The flowers have four sepals, four petals, and eight stamens, ap-

parently diplostemonously arranged. Between the stamens there is an eight-lobed disk-like structure (Fig. 36). The ovary is semi-inferior and three-loculed, with numerous ovules. There are three free thick styles. The flower type is represented by only a few incompletely preserved specimens and the structure is not fully known. The characters of the fossils suggest, however, a close relationship with some modern plants of the Saxifragales, e.g., the Hydrangeaceae.

1.4. Epigynous flowers with haplostemonous androecium. 1.4.1. Anthers antipetalous. The fossil flowers illustrated in Figures 25–28 were partly described by Friis and Skarby (1982). Additional material has since provided information on the corolla and the androecium. The flowers are small (about 3 mm long), bisexual, and actinomorphic, with an almost epigynous perianth insertion. There are five free sepals and five free petals, which are rarely preserved. The androecium is composed of five antipetalous stamens in one whorl; the anthers are dorsifixed and open by longitudinal slits (Figs. 25, 27). Pollen grains have not been observed yet. There is a pronounced five-lobed disk (Fig. 26). The ovary is inferior, two-loculed, and formed by two fused carpels. There are two free, thick styles (Fig. 26). The placentation is central with many anatropous ovules (Fig. 28). The surface of the ovary is characterized by distinct longitudinal ridges. Like *Scandianthus*, the fossil flower is believed to have been pollinated by insects because of the pronounced, perhaps nectariferous disk. This floral type also shares many characters with modern members of the Saxifragales and is believed to belong to this group.

1.4.2. Anthers antisepalous. Among the Swedish fossils two different flower types with antisepalous stamens have been recognized. The flower type shown in Figures 29 and 30 is probably also related to the Saxifragales. The flowers are small (1–2 mm long), bisexual, and with a more or less epigynous perianth insertion. The perianth is composed of five free petals and five free sepals of open aestivation. There are five antisepalous stamens; the filaments are triangular, almost of the same size as the petals (Fig. 29). Anthers have not been found attached to the filaments. The pistil is bicarpellary; its ovary is semi-inferior and one-loculed, and its style is simple. The fruit is a capsule dehiscing along the midline of the carpels. The placentae are parietal with many anatropous ovules (Fig. 34). The seeds are small and have a thin seed coat.

The fossil flowers have many characters in common with those of *Scandianthus*, but differ in having only one whorl of stamens and a single style. Flowers of similar construction also occur in some modern plants of the Saxifragalean complex, and these fossil flowers should probably also be referred to this group. However, a more detailed study of their systematical affinity is needed before the final affiliation can be made.

Another group of flowers from the Swedish material represented by many well-preserved specimens is illustrated in Figures 31–33. The flowers are about 1–2 mm long, bisexual with radial symmetry. The perianth is epigynous composed of five free sepals and five free petals. There is one whorl of antisepalous stamens. The filaments are thread-like and the dorsifixed anthers open by longitudinal slits (Fig. 33). Pollen grains have not been observed. Between the stamens and style there is apparently a broad disk. The ovary is inferior and unilocular, formed by two carpels, and with one style. The placentae are parietal and marginal, with few anatropous ovules (Fig. 32). The mature fruit is an elongated capsule, apparently with only one or two seeds. It dehisces along the midline of the carpels starting at the base. Figure 34 illustrates a minute epigynous, pentamerous flower about 0.7 mm long with well-preserved stamens. It possibly represents an immature stage of the flowers described above. The flowers show some features comparable to those of some modern plants of the Rosanae and Myrtanae, but a detailed comparative study has not yet been carried out.

2. *Monochlamydous flowers*. The Swedish material includes a few floral types that bear only one whorl of perianth parts. They are all epigynous with a one-loculed ovary, and one basal and orthotropous seed. They produced small triporate pollen grains assignable to the Normapolles complex. The flowers are probably closely related and belong to the same group. Based on the number of parts and floral symmetry, they are grouped into three different genera. The simple construction of the flowers and the structure of the pollen grains indicate that these flowers were adapted to wind-pollination.

Dispersed pollen forms included in the Normapolles complex (Pflug, 1953; Góczán et al., 1967) occur as significant elements of many Upper Cretaceous and Lower Tertiary palynofloras of Europe and North America (Góczán et al., 1967; Zaklinskaya, 1981; Tschudy, 1981). Pollen grains of the Normapolles type are also abundant

in the Upper Cretaceous fluviatile deposits of Sweden (Skarby, 1968), and anthers including Normapolles pollen have been recovered among the megafossil plants from Sweden. The fossil flowers from Sweden represent the first megafossil evidence of plants producing this stratigraphical important pollen group.

Comparison with modern plant groups shows that the fossil flowers and fruits share characters with modern Juglandales (Juglandaceae and Rhoipteleaceae) and Myricales (Myricaceae). These families generally include unisexual flowers, but bisexual flowers occur in *Rhoiptelea* (Rhoipteleaceae) and *Canacomyrca* (Myricaceae). However, the fossils cannot with certainty be placed in any of these families, and it is thought that they represent an intermediate, perhaps ancestral, group with bisexual flowers (Friis, 1983).

2.1. *Epigynous, pentamerous flowers with radial flower symmetry*. This organizational type is represented in the Swedish material by one species of *Manningia* Friis (1983) (Figs. 7, 37–39). The structure is known from several developmental stages from small flowers to mature fruits. The flowers are bisexual and actinomorphic with an epigynous perianth composed of five free tepals in one whorl. The androecium is composed of five antitepalous stamens. No anthers in the preserved material are attached to the filaments of the flower, but fragments of pollen sacs with pollen and numerous dispersed pollen grains have been found inside the perianth of many flowers (Fig. 39). The pollen grains all belong to the same type. They are peroblate and triangular, about 20 microns in equatorial diameter, with pronounced thickenings at the inner apertures and with elongated outer apertures. They are assignable to the Normapolles genus *Trudopollis* Pflug (1953).

The ovary is inferior, one-loculed, and formed by three fused carpels. There is one thick style with three elongated stigmatic branches. The fruit is a nut with a single basal and orthotropous seed.

2.2. *Epigynous, hexamerous flowers with radial symmetry*. One fossil species, *Antiquocarya verruculosa* Friis (1983), representing this structural type has been recovered among the Swedish fossils (Figs. 8, 43, 44). The flowers are bisexual and actinomorphic, with an epigynous perianth composed of six small, apparently reduced tepals (Fig. 43). The androecium is haplostemonous with six antitepalous stamens. The stamens are represented only by remnants of filaments: anthers have not been observed. In a

single specimen, pollen grains referable to the Normapolles group have been observed attached to the surface of the styles. The ovary is epigynous, one-loculed, and composed of three fused carpels. There are three very short styles, the stigmatic parts of which have not been preserved (Fig. 44). The fruit is a nut with one basal, orthotropous seed.

A very similar floral structure has been observed in the fossil flowers illustrated in Figures 45 and 46, but these flowers are apparently naked. Traces of a perianth have not been observed in any of the specimens studied (more than 50), and it is believed that they represent a reduced (apochlamydous) form of the flower illustrated in Figures 43 and 44. The flowers bear remnants of six stamens at the top of the ovary (Fig. 46), but anthers have not been preserved. Pollen grains referable to the Normapolles group have also been found in these flowers, attached to the surface of the apical part. The ovary is one-loculed, formed by three carpels, and has one orthotropous and basal ovule.

2.3. Epigynous, bimerous and bisymmetrical flowers. This floral type has been studied from numerous small nuts with persistent floral parts (Figs. 9, 40–42). It is very common in certain horizons of the fluviatile sequence and so far several thousands of specimens have been found.

The material includes three species apparently in one genus, *Caryanthus* Friis (1983). The flowers are bisexual and bisymmetrical with epigynous perianth insertion. The ovary is enclosed by two thick bracteoles and a small bract united with the base of the ovary. The perianth is epigynous with four tepals in two decussate pairs. The androecium is composed of six stamens. No anthers have been observed attached to the filaments, but pollen grains of the Normapolles type have been found inside the perianth of many specimens (Fig. 40). The pollen grains are peroblate, triangular, with protruding apertures. The outer apertures are elongated and there is a tri-radiate fold over the polar area. These grains are referable to the Normapolles genus *Plicapollis*.

The ovary is inferior and one-loculed, formed by two fused carpels. The carpels are apparently transverse. There are two styles or stigmatic branches and a single basal and orthotropous seed. The seed coat is thin and membranous.

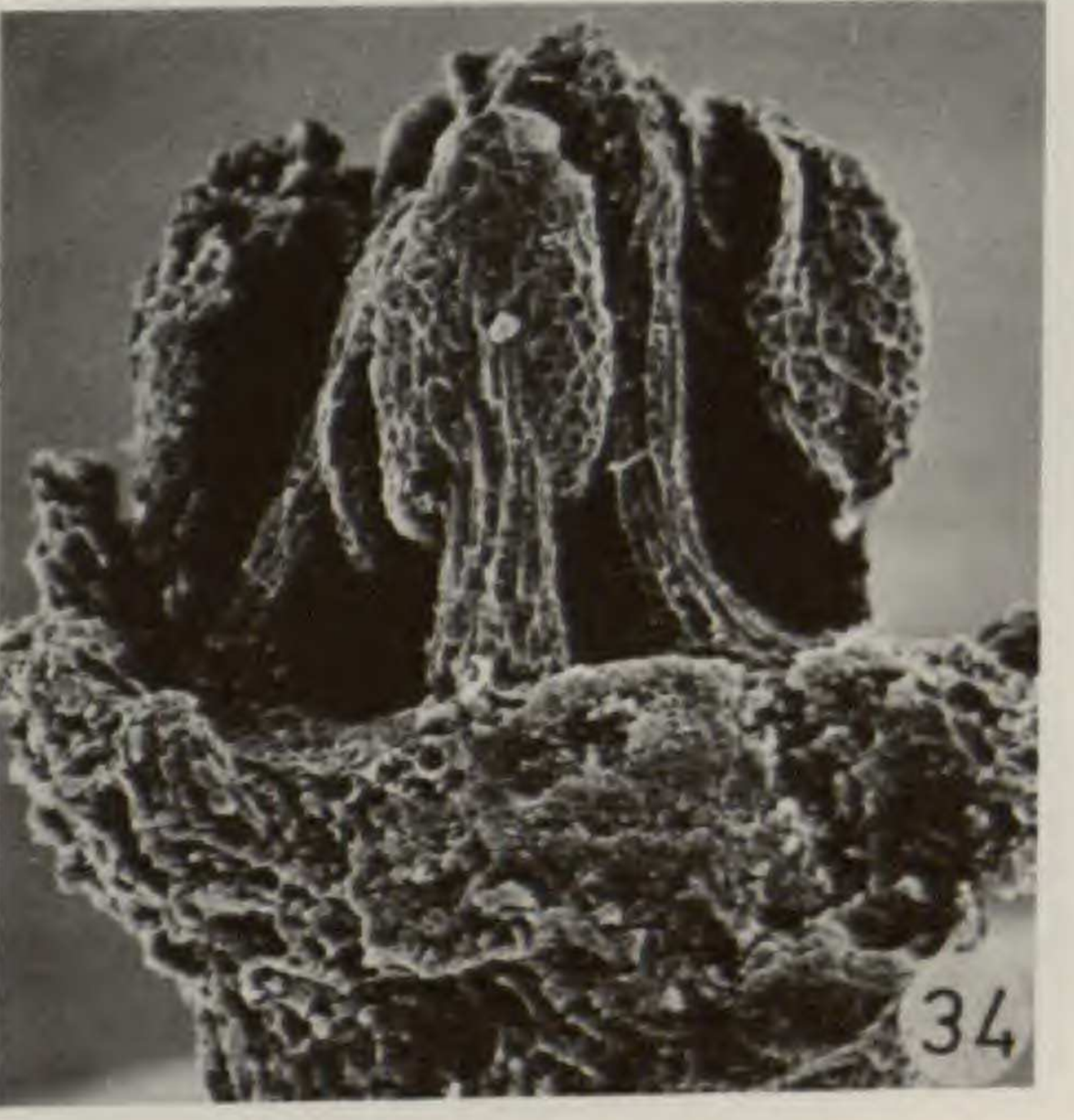
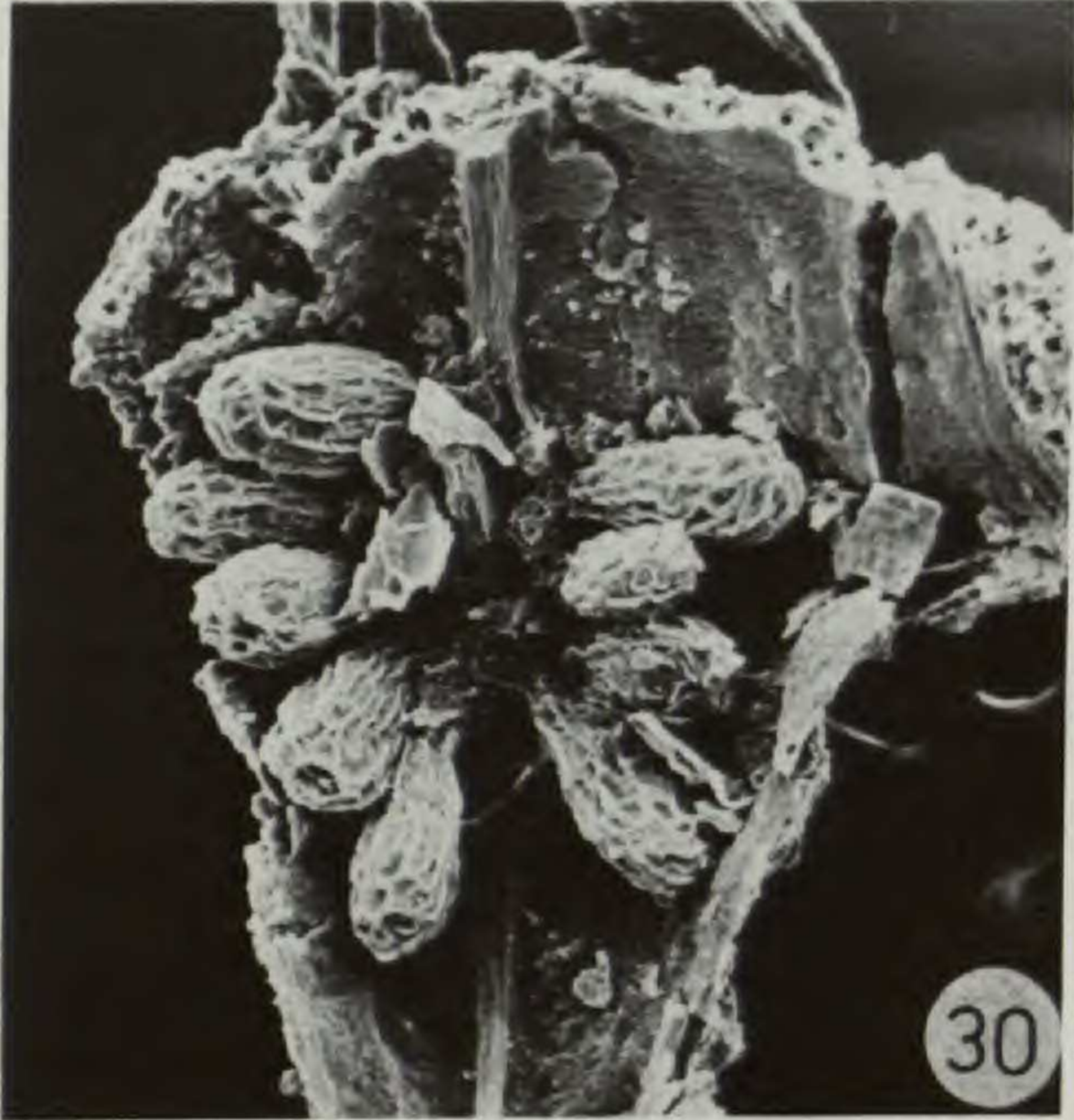
DISCUSSION

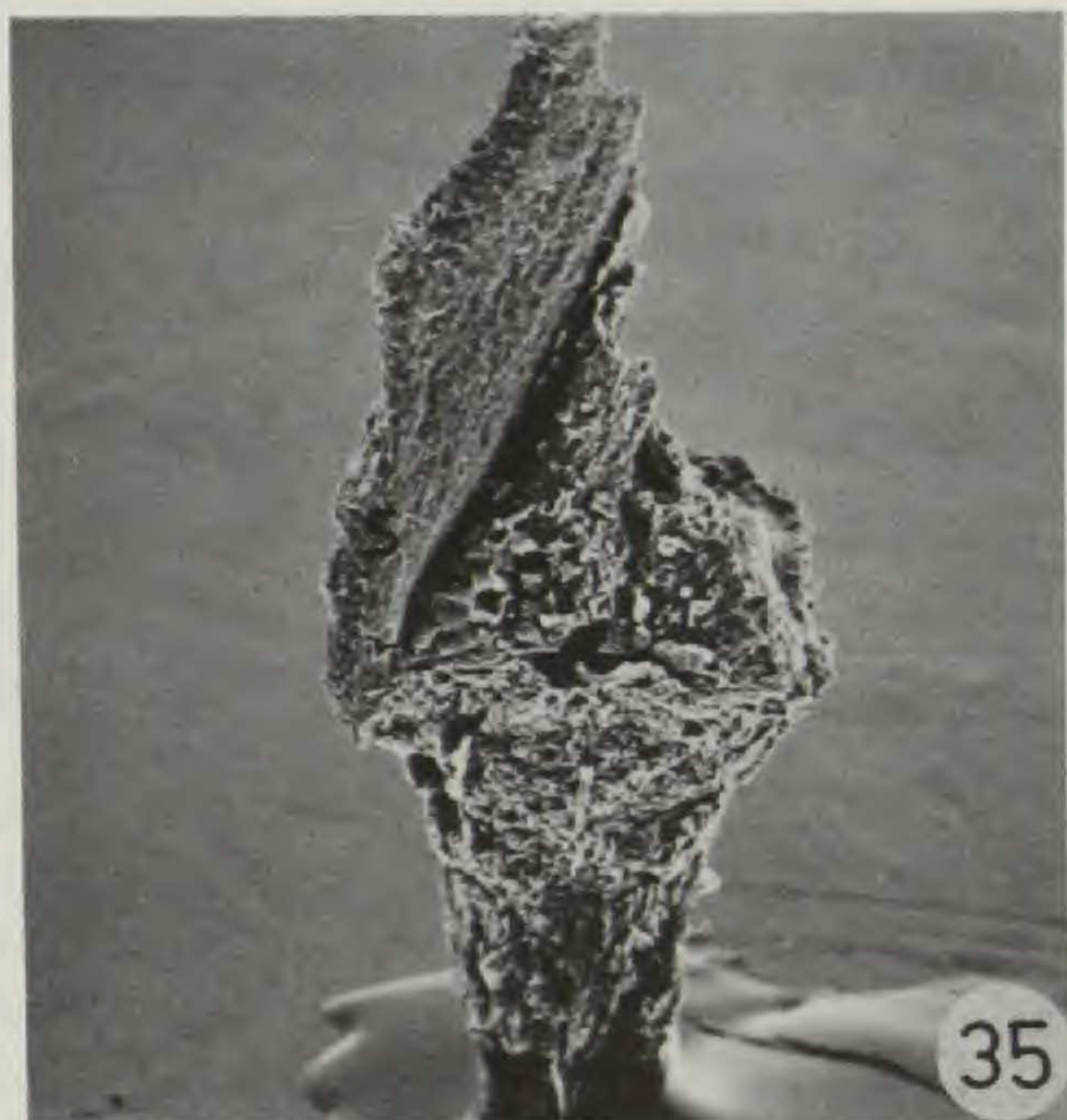
The examination of the plant megafossils from Åsen demonstrates the existence in the Upper Cretaceous of a great morphological diversification of the angiosperm reproductive structure. The fossil flowers studied are mainly actino-

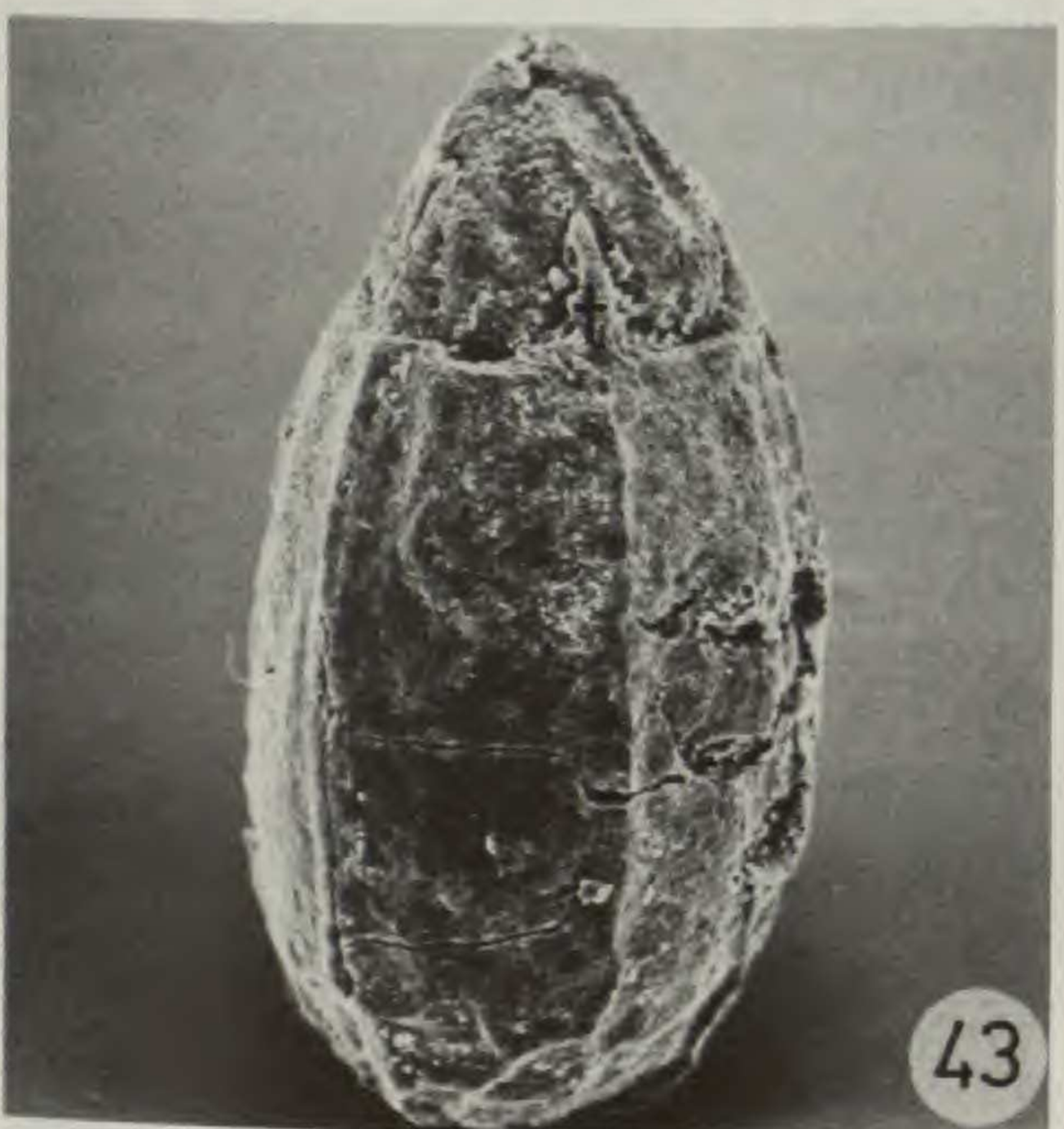
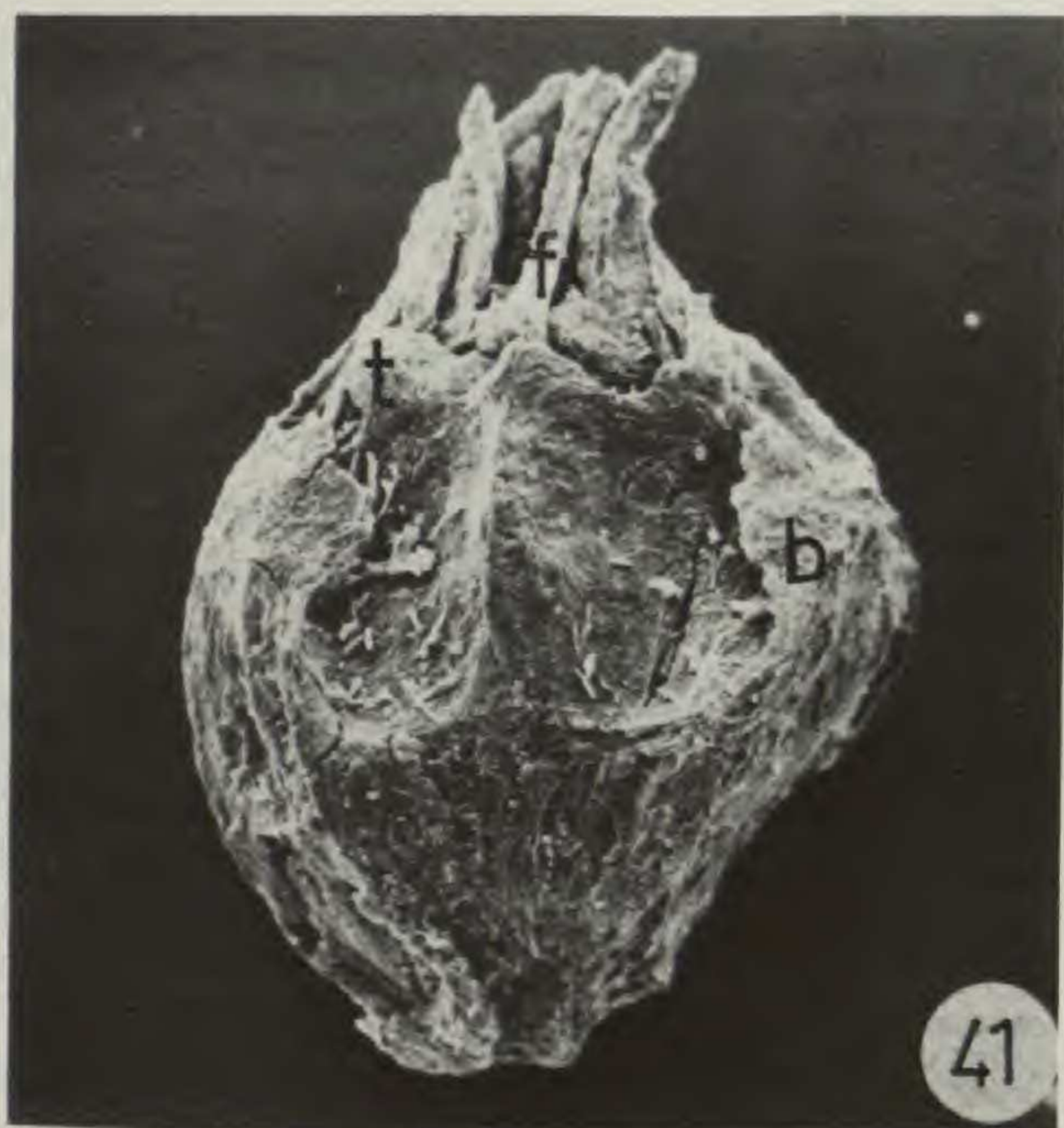
FIGURES 29–34. Fossil flowers from the Upper Cretaceous of Sweden. 29–30. Heterochlamydous, epigynous flower with haplostemonous androecium (floral diagram see Fig. 6).—29. Flower with remnants of sepals (s), petals (p), and stamens (f) preserved; SEM-197₂, ×75.—30. Section of flower showing parietal placenta with many anatropous seeds; SEM-203₇, ×85. 31–33. Heterochlamydous, epigynous flower with haplostemonous androecium.—31. Flower with single stamen preserved; SEM-192, ×70.—32. Section of flower showing parietal placenta with anatropous ovules; SEM-197₁, ×75.—33. Apical view of flower showing petals (p) and stamen (f and a); same specimen as Figure 31, ×85.—34. Small flower bud with stamens and style; SEM-198, ×180.

FIGURES 35–40. Fossil flowers, fruits and pollen from the Upper Cretaceous of Sweden. 35–36. Heterochlamydous, epigynous and tetramerous flower (floral diagram see Fig. 3).—35. Flower with sepal (s) and petal (p) preserved; SEM-214₁, ×45.—36. Apical view of flower showing remnants of petals (p), stamens (f), and styles (st); SEM-213₄, ×20. 37–39. *Manningia crassa* Friis, monochlamydous flower with pentamerous perianth (floral diagram see Fig. 8).—37. Flower bud with tepals (t) and clusters of pollen preserved; SEM-176₁, ×40.—38. Apical view of fruit with remnants of tepals (t) and stamens (f); SEM-179₁, ×85.—39. Pollen grains of the Normapolles type (*Trudopollis*) from apical part of flower bud; same specimen as Figure 37, ×1,700.—40. Pollen grains of the Normapolles type (*Plicapollis*) from apical part of *Caryanthus knoblochii*; SEM-164₃, ×3,850.

FIGURES 41–46. Fossil flowers and fruits from the Upper Cretaceous of Sweden. 41–42. *Caryanthus knoblochii* Friis, monochlamydous, epigynous and bimerous flower (floral diagram see Fig. 7).—41. Fruit with remnants of bracteoles (b), tepals (t), and stamens (f); SEM-164₁, ×55.—42. Apical view of fruit with remnants of six stamens (f); SEM-165₃, ×70. 43–44. *Antiquocarya verruculosa* Friis, monochlamydous, epigynous and hexamerous flower (floral diagram see Fig. 9).—43. Fruit with persistent tepals (t) and remnants of stamens; SEM-212₁, ×55.—44. Apical view of fruit showing position of perianth and stamens; same specimen as Figure 43, ×100. 45–46. *Antiquocarya nuda*, apochlamydous flower (?).—45. Fruit with scars from stamens (f); SEM-200₃, ×45.—46. Apical view of fruit showing position of stamens and three styles; SEM-200₁, ×45.







morphic. One group of bisymmetrical flowers with a simple perianth represents, so far, the first occurrence of this type of floral symmetry. According to Dilcher (1979), all mid-Cretaceous floral structures found exhibit radial symmetry (actinomorphic). No zygomorphic or asymmetrical fossil flowers have been described yet. However, evidence from fossil fruits and pollen may indicate that zygomorphic flowers developed during the Maastrichtian and early Tertiary (e.g., Caesalpinaceae, Chandler, 1961; Muller, 1981), and that asymmetrical flower types appeared late in the Tertiary (e.g., Valerianaceae, Łańcucka-Środoniowa, 1979; Muller, 1981).

The fossil flowers from Åsen are all cyclic with a definite number of parts. Polymerous flowers with helically arranged parts generally considered the ancestral type of the angiosperms (e.g., Dahlgren, 1983) have not been recognized. However, the presence of small, stalked follicles with decurrent stigmas comparable to fruits of some modern Ranunculaceae may suggest that this flower type also existed in the Upper Cretaceous flora of Sweden. Records of an elongated fruiting axis with helically arranged follicles indicate that this flower type had developed in the late early Cretaceous (Dilcher, 1979; Vachrameev & Krasilov, 1979).

The majority of fossil flowers from Åsen are epigynous, and the material includes only a single perigynous and a few hypogynous types. They differ in this respect from the mid-Cretaceous floral structures, which are generally hypogynous. However, the record of a fossil fruit with persistent calyx, *Kalinaia decapetala* Bayer (1914), from Czechoslovakia may indicate that epigynous flowers had evolved as early as the Cenomanian.

The fossil material includes heterochlamydous flowers with a well-developed disk indicating adaptation to insect-pollination as well as simple constructed monochlamydous flowers apparently adapted to wind-pollination.

Although there is no indication of unisexual flowers among the Upper Cretaceous fossils from Sweden, several mid- and Upper Cretaceous records of small flowers in spikes or heads referred to e.g., the Platanaceae and the Myricaceae (Velenovský, 1889; Velenovský & Viniklár, 1926, 1929; Krassilov, 1973, 1977; Dilcher, 1979) indicate that unisexual flowers developed early in the history of the angiosperms.

The present investigation has revealed a variety of floral types, which mainly represent the

subclasses Rosidae and Hamamelidae (sensu Takhtajan, 1980). The Dilleniidae is represented by a single flower type related to the Theaceae. This is consistent with the taxonomical results obtained from the study of the fossil pollen record (Muller, 1970, 1981). According to Muller (1981), the period Coniacian-Campanian (Muller's floral phase IIIb) is characterized by a strong diversification of the Hamamelidae and to a lesser degree diversification of the Rosidae, and also by the appearance of the Dilleniidae. Thus, the fossil flowers studied probably reveal the major morphological diversification of the angiosperm flower reached by the mid-Senonian.

LITERATURE CITED

- BASINGER, J. F. 1976. *Paleorosa similkameensis*, gen. et sp. nov., permineralized flowers (Rosaceae) from the Eocene of British Columbia. *Canad. J. Bot.* 54: 2293-2305.
- BAYER, E. 1914. Fytopalaeontologicke přispěvky ku Poznání českých křidových vrstev peruckých. *Arch. Přír. Výzk. Čech* 25: 1-66.
- CASPARY, R. 1872. Einige Pflanzenreste aus der Bernsteinzeit. *Schriften Königl. Phys.-Ökon. Ges. Königsberg* 12(Jahrg. 1872): 28.
- . 1881a. Einige pflanzliche Abdrücke und Einschlüsse in Bernstein. *Schriften Königl. Phys.-Ökon. Ges. Königsberg* 21(Jahrg. 1880): 28-30.
- . 1881b. Über neue fossile Pflanzen der blauen Erde, d.h. des Bernsteins, des Schwarzharzes und des Braunharzes. *Schriften Königl. Phys.-Ökon. Ges. Königsberg* 22(Jahrg. 1881): 22-27.
- CHANDLER, M. E. 1961. The Lower Tertiary Floras of Southern England I. British Museum (Natural History), London.
- CHITALEY, S. D. & M. Z. PATEL. 1975. *Raoanthus intertrappea*, a new petrified flower from India. *Palaeontographica, Abt. B, Paläophytol.* 153: 141-149.
- COLIN, J.-P. 1973. Microfossiles vegetaux dans le Cenomanien et le Turonien de Dordogne (S.O. France). *Palaeontographica, Abt. B, Paläophytol.* 143: 106-119.
- CONWENTZ, H. 1886. Die Flora des Bernsteins, 2. Die Angiospermen des Bernsteins. Commissions-Verlag von Wilh. Engelmann, Leipzig.
- CRANE, P. R. & D. L. DILCHER. 1984 [1985]. *Lesqueria*: an early angiosperm fruiting axis from the mid-Cretaceous. *Ann. Missouri Bot. Gard.* 71: 384-402.
- CREPET, W. L. & C. P. DAGHLIAN. 1980. Castaneoid inflorescences from the Middle Eocene of Tennessee and the diagnostic value of pollen (at the subfamily level) in the Fagaceae. *Amer. J. Bot.* 67: 739-757.
- & D. L. DILCHER. 1977. Investigations of angiosperms from the Eocene of North America: a mimosoid inflorescence. *Amer. J. Bot.* 64: 714-725.

- , C. P. DAGHLIAN & M. ZAVADA. 1980. Investigations of angiosperms from the Eocene of North America: a new Juglandaceous catkin. *Rev. Palaeobot. Palynol.* 30: 361–370.
- DAGHLIAN, C. P., W. L. CREPET & T. DELEVORYAS. 1980. Investigations of Tertiary angiosperms: a new flora including *Eomimosoidea plumosa* from the Oligocene of Eastern Texas. *Amer. J. Bot.* 67: 309–320.
- DAHLGREN, R. 1983. General aspects of angiosperm evolution and macrosystematics. *Nordic J. Bot.* 3: 119–149.
- DILCHER, D. L. 1979. Early angiosperm reproduction: an introductory report. *Rev. Palaeobot. Palynol.* 27: 291–328.
- & J. F. BASINGER. 1980. [Abstract:] Bisexual flowers from the mid-Cretaceous. *Abstr. Int. Palaeobot. Conf., Reading.* 13.
- & P. R. CRANE. 1984 [1985]. *Archaeanthus*: an early angiosperm from the Cenomanian of the Western Interior of North America. *Ann. Missouri Bot. Gard.* 71: 351–383.
- , W. L. CREPET, C. D. BEEKER & H. C. REYNOLDS. 1976. Reproductive and vegetative morphology of a Cretaceous angiosperm. *Science* 191: 854–856.
- FRIIS, E. M. 1983. Upper Cretaceous (Senonian) floral structures of Juglandalean affinity containing Normapolles pollen. *Rev. Palaeobot. Palynol.* 39: 161–188.
- & A. SKARBY. 1981. Structurally preserved angiosperm flowers from the Upper Cretaceous of Southern Sweden. *Nature* 291(5815): 485–486.
- & ———. 1982. *Scandianthus* gen. nov., angiosperm flowers of Saxifragalean affinity from the Upper Cretaceous of Southern Sweden. *Ann. Bot. (London)* n.s. 50: 569–583.
- GÓCZÁN, F., J. J. GROOT, W. KRUTZSCH & B. PACLTÓVA. 1967. Die Gattungen des 'Stemma Normapolles Pflug 1953b' (Angiospermae). *Neubeschreibungen und Revision europäischer Formen (Oberkreide bis Eozän)*. *Paläontol. Abh., Abt. B, Paläobot.* 3: 427–633.
- GOEPPERT, H. R. & G. C. BERENDT. 1845. *Der Bernstein und die in ihm befindlichen Pflanzenreste der Vorwelt*. Berlin.
- HALL, J. W. 1963. Megaspores and other fossils in the Dakota Formation (Cenomanian) of Iowa, (U.S.A.) (I). *Pollen & Spores* 5: 425–443.
- HARPER, J. L., P. H. LOVELL & K. G. MOORE. 1970. The shapes and sizes of seeds. *Annual Rev. Ecol. Syst.* 1: 327–356.
- JUNG, W., H.-H. SCHLEICH & B. KÄSTLE. 1978. Eine neue, stratigraphisch gesicherte Fundstelle für Angiospermen-Früchte und -Samen in der oberen Gosau Tirols. *Mitt. Bayer. Staatssamml. Paläontol. Hist. Geol.* 18: 131–142.
- KNOBLOCH, E. 1964. Neue Pflanzenfunde aus dem südböhmischen Senon. *Jahrb. Staatl. Mus. Mineral. Dresden* 1964: 133–201.
- . 1971. Fossile Früchte und Samen aus der Flyschzone der mährischen Karpaten. *Sborn. Geol. Věd. Paleontol.* 13: 7–43.
- . 1977. Fossile Pflanzenreste aus der Kreide und dem Tertiär von Österreich. *Verh. Geol. B.-A. Jahrg.* 1977, 3: 415–426.
- KRASSILOV, V. A. 1973. Upper Cretaceous staminate heads with pollen grains. *Palaeontology* 16: 41–44.
- . 1977. The origin of angiosperms. *Bot. Rev. (Lancaster)* 43: 143–176.
- ŁAŃCUCKA-ŚRODONIOWA, M. 1979. Macroscopic plant remains from the freshwater Miocene of the Nowy Sącz Basin (West Carpathians, Poland). *Acta Palaeobot.* 20: 3–117.
- LARSSON, S. G. 1978. *Baltic Amber—A Palaeobiological Study*. Scandinavian Science Press Ltd., Klampenborg.
- MINER, E. L. 1935. Paleobotanical examinations of Cretaceous and Tertiary coals. I. Cretaceous coals from Greenland. *Amer. Midl. Naturalist* 16: 595–615.
- MONTEILLET, J. & J.-R. LAPPARTIENT. 1981. Fruits et graines du Crétacé supérieur des carrières de Paki (Sénégal). *Rev. Palaeobot. Palynol.* 34: 331–344.
- MULLER, J. 1970. Palynological evidence on early differentiation of angiosperms. *Biol. Rev. Biol. Proc. Cambridge Philos. Soc.* 45: 417–450.
- . 1981. Fossil pollen record of extant angiosperms. *Bot. Rev. (Lancaster)* 47: 1–142.
- PFLUG, H. D. 1953. Zur Entstehung und Entwicklung des angiospermiden Pollens in der Erdgeschichte. *Palaeontographica, Abt. B, Paläophytol.* 95: 60–171.
- PRAKASH, V. 1956. On the structure and affinities of *Sahnipushpam glandulosum* sp. nov. from the Deccan Intertrappean series. *Palaeobotanist* 4: 91–100.
- SCHEMEL, M. P. 1950. Cretaceous plant microfossils from Iowa. *Amer. J. Bot.* 37: 750–754.
- SHUKLA, V. B. 1944. On *Sahnianthus*, a new genus of petrified flowers from the Intertrappean Beds at Mohangan Kalan in the Deccan and its relation with the fruit *Enigmocarpon parijai* Sahnii from the same locality. *Proc. Natl. Acad. Sci. India, Sect. B, Biol. Sci.* 14: 1–39.
- SKARBY, A. 1968. *Extratropopollenites* (Pflug) emend. from the Upper Cretaceous of Scania, Sweden. *Acta Univ. Stockholm.* 16: 1–60.
- STEBBINS, G. L. 1974. *Flowering Plants—Evolution Above the Species Level*. Belknap Press of the Harvard Univ. Press, Cambridge.
- STOPES, M. C. & K. FUJII. 1911. Studies on the structure and affinities of Cretaceous plants. *Philos. Trans., Ser. B*, 201: 1–90.
- TAKHTAJAN, A. J. 1980. Outline of the classification of flowering plants (Magnoliophyta). *Bot. Rev. (Lancaster)* 46: 225–359.
- TIFFNEY, B. H. 1977. Dicotyledonous angiosperm flower from the Upper Cretaceous of Martha's Vineyard, Massachusetts. *Nature* 265(5590): 136–137.
- . 1984 [1985]. Seed size, dispersal syndromes and rise of the angiosperms: evidence and hypothesis. *Ann. Missouri Bot. Gard.* 71: 551–576.
- TSCHUDY, R. H. 1981. Geographic distribution and dispersal of Normapolles genera in North America. *Rev. Palaeobot. Palynol.* 35: 283–314.
- VACHRAMEEV, V. A. & V. A. KRASSILOV. 1979. Reproductivnyye organy tsvetkovykh iz al'ba Kazakhstana. *Paleontol. Žurn.* 1979: 121–128.

- VANGEROW, E. F. 1954. Megasporen und andere pflanzliche Mikrofossilien aus der Aachener Kreide. *Palaeontographica*, Abt. B, Paläophytol. 96: 24-38.
- VELENOVSKÝ, J. 1889. Květena Českého Cenomanu. *Abh. Königl. Böhm. Ges. Wiss.*, Ser. 7, 3: 1-75.
- & L. VINIKLÁŘ. 1926. *Flora cretacea bohemiae*. Part 1. Czechoslovakia Statního Geol. Ústavu. Rozpr. 1-54.
- & ———. 1927. *Flora cretacea bohemiae*. Part 2. Czechoslovakia Statního Geol. Ústavu Rozpr. 1-51.
- & ———. 1929. *Flora cretacea bohemiae*. Part 3. Czechoslovakia Statního Geol. Ústavu Rozpr. 1-31.
- & ———. 1931. *Flora cretacea bohemiae*. Part 4. Czechoslovakia Statního Geol. Ústavu Rozpr. 1-112.
- ZAKLINSKAYA, E. D. 1981. Phylogeny and classification of the Normapolles. *Rev. Palaeobot. Palynol.* 35: 139-147.